REGENERATION IN PLANTS

JOHN M. COULTER, PH.D.
Professor of Botany, University of Chicago

Theology, in the nature of the case, must use analogies to express the relation between man and God. In the past religious analogies have been those of politics, of paternity, or of law. The rise of the biological sciences has affected all types of thinking and has given a new group of analogies as well as technical terms to other sciences than this. It is in the hope of assisting theology to appropriate this dominant type of thinking that the BIBLICAL WORLD *will occasionally print articles dealing with biological matters. The present article by a distinguished botanist contains a description of the life process, which abounds in suggestive parallels to that of spiritual life. Indeed, one cannot help inquiring whether they may not be something more than analogies.*

This title does not contain the implication that regeneration does not occur among animals, but simply that the facts in reference to it with which I am most familiar have been obtained from experimental work with plants. Attention was called to the phenomenon of regeneration probably first in connection with animals, when in 1744 Trembley sectioned hydras in various ways, and found that each piece was able to produce the lost parts. Later, similar experiments were performed with worms, as the earth worms. It was found that if such a worm be cut in two, the tail end produces a head, and the head end a tail. As the experimental study of regeneration was extended to include other animals and plants, the application of the term became extended, and somewhat indefinite. It is necessary, therefore, to define regeneration.

Strictly, regeneration means the restoration of a part that has been removed. For example, if a starfish loses an arm, a new arm is developed. If a root tip is cut off not far from the apex, a new tip is developed. The cells of the cut surface grow and restore the lost part. If the apex of the growing frond of certain ferns is split, each half re-forms the removed half. In these cases regeneration is strictly the restoration of a lost part.

On the other hand, if a root tip be cut farther back than in the case mentioned above, the cells of the cut surface do not form a new tip, but the cells behind organize a new growing point, and a new root replaces the old one that was mutilated. In many cases, if a stem is cut away from a root, the stump of the stem does not grow and replace the lost parts, but an entirely new stem arises from the root. Likewise most stems when removed from roots can be made to produce new roots. In all these cases there is not strictly a restoration of lost parts, but the development of a new structure that replaces the old one. In other words, it is replacement rather than restoration; but so far as the working body of the plant as a whole is concerned, it amounts to the same thing.

Another situation must be included. In trimming trees, for example, if the tip of the tree or of a branch is cut off, new branches arise, but none of them would have appeared if the old branch tips had not been removed. In this case, however, the new branches arise from what are called latent buds, growing points already organized, but prevented from developing by the growth of the old branches. The new branches replace the old ones, but they are not formed *de novo;* their primordia already exist and are simply stimulated to growth.

There are, therefore, at least three distinct categories included in what is called regeneration: (1) the literal restoration of a lost part, so that the old organ or structure is mended; (2) the organization of a new structure that replaces the old one; and (3) the stimulation into growth of an organ already started, but for some reason forbidden to develop. These categories make it evident that regeneration merges insensibly into ordinary vegetative growth, and that regeneration is not really different from ordinary growth.

This leads necessarily to an explanation of what growth means. The body of a plant consists of an innumerable number of units, called cells. The term cell is misleading, for the real unit is an organized bit of the living substance (protoplasm) called the protoplast, which in plants usually incases itself with a wall. Protoplasm is the material, and the protoplast is a definite organization of this material; in other words, it might be regarded as protoplasm individualized. The living plant body, therefore, is a congeries of protoplasts, not isolated within their cell walls, but communicating with one another by protoplasmic strands. All the protoplasts, therefore, are in living connection. This fact is necessary to know if one is to understand how one part of a plant can affect another part.

Among the many powers that belong to protoplasts, the one that relates to this discussion is the power of self-division. A protoplast divides in such a way that each of the two new protoplasts contains an equal share of every structure that belonged to the parent protoplast. The mechanism by which this equal division is accomplished is one of the most elaborate and interesting mechanisms known in plants and animals. The new protoplasts enlarge until they equal in size the parent protoplast, and thus two new cells replace one old cell. This means growth, but it is also the fundamental process of reproduction and inheritance. It is a function of a protoplast, therefore, to divide and to produce new cells, and in so doing to pass on to the new cells its own structure. In a plant body, however, many cells become what are called permanent cells, forming permanent tissue, which means that they do not divide to form new cells. It does not follow that such cells have lost the power of division, for almost any permanent cells can be stimulated to division, and thus become dividing cells again.

It is easy to follow the successive generations of dividing cells as they build up an organ or a structure of the body, but the baffling problem as yet is the far-reaching, directing influence that determines the particular kind of organ or structure which these dividing cells

build. The important things to remember, however, so far as regeneration is concerned, are that any protoplast can produce new cells; that it can be stimulated into division even if it has ceased dividing; and that the generations of cells it produces may form a complete organ or structure.

It is as difficult to distinguish regeneration from reproduction as to distinguish it from growth. It is very common for a group of vegetative cells to produce a new individual. In fact, much of our plant culture depends upon this. A potato tuber and a hyacinth bulb are merely aggregates of vegetative cells, but under certain conditions they produce new individuals, which is what is technically called reproduction. Spores and eggs, which are single cells, show the same power. The difference between reproduction and regeneration, therefore, is simply that in regeneration certain lost parts are restored or replaced, while in reproduction all the parts are gone, and therefore all the parts are reproduced.

It is obvious, therefore, that cell division is the fundamental process which results in growth, in regeneration, or in reproduction; it produces a new individual, or it repairs an old individual, or it merely causes an individual to grow. This statement fits regeneration into its setting as simply one expression of a general power which belongs to all protoplasts.

When the phenomena of regeneration began to accumulate, some explanation was sought. If regeneration had been associated at first with growth and reproduction, as simply one expression of a general power possessed by all protoplasts, many of the "explanations" would never have been advanced. For example, it was suggested that regeneration is caused by the wound stimulus; that is, the very act that removes a structure arouses the remaining cells to an activity that restores it. Another suggestion was that the loss of a part necessarily disturbs the nutritive relations of a plant, and this results in a growth stimulus. It was also proposed that changes in the water content of a plant, resulting from a loss of a part, might also result in the unusual growth represented by regeneration. These are but samples of the many "explanations" advanced; some of them resting upon a considerable body of evidence, and some of them purely speculative.

When the problem was taken up seriously and completely, and all the proposed explanations tested, one by one, the case seemed to become clear. The wound stimulus, the disturbed nutritive relations, the change in water content, and the whole brood of "explanations" were proved to be entirely inadequate. Investigators began to realize the relationship of regeneration to growth and reproduction, and, therefore, that the explanation of it must be due chiefly to inherent powers in the plant itself.

It will be remembered that when a part is removed, as in the pruning of trees, dormant primordia are stimulated to develop which otherwise would remain dormant. At the same time, the removal of a part, as a stem or a root, starts the development of primordia when they do not exist. Still further, it was found by experiment that one does not have to remove one structure so

that another may be allowed to develop, but he can accomplish the same thing by preventing a structure from functioning, which is equivalent to its removal so far as regeneration is concerned. This, of course, would dispose necessarily of the wound stimulus idea. The real picture of a plant body, therefore, is that it is made up of innumerable growing points, either organized or potential, and that these growing points are held in check by the parts already growing. The failure of many growing points of a plant to develop has been found to be due, not to lack of conditions that favor growth, as nutrition and moisture, or to such external stimuli as light and gravity, or to any lack of suitable food material, but to some influence independent of all these, which one organ is able to exert over other parts, and so prevent their growth. If such an organ is removed, then growth of the inhibited structures occurs. The very act of growth of one part, therefore, forbids the growth of numerous structures which could replace it. What this inhibiting influence is that one organ exerts over other parts of the body, one can hardly imagine, but it is entirely probable that it acts along the protoplasmic connections which put all the protoplasts into one living system. A potential growing point is nothing but a group of protoplasts anywhere in the body, and these protoplasts are not so much stimulated into growth, as permitted to grow by the removal of some structure that has prevented their development.

A somewhat more detailed account of regeneration as shown in *Zamia* may make the facts more definite. *Zamia* is a small cycad that grows abundantly in Florida. The body resembles a woody turnip or radish, bearing a crown of leaves above, and sending out roots below. It was noticed in the field that when the top of the stem was sliced off with a hoe, a new crown would develop. The plant, therefore, seemed to be a favorable one for some experimental work on regeneration. The crude field observations were verified, and in every case a decapitated body, if kept in growing conditions, developed a new top with its crown of leaves. This was a case of strict regeneration; that is, the restoration of a lost part, the new structure becoming an integral part of the old. There was no stimulating into development a new structure sprouting out of the old to replace it, but the mutilated body was made whole again. Moreover, the lost part was not a subordinate one, but the most prominent and important part of the plant.

The process of regeneration was observed in detail, and was as follows. Through the center of the body there extends a hollow woody cylinder, called the vascular cylinder because it is a conducting system, transporting water and the various elaborated foods. At the top of the stem this cylinder domes over, so that it underlies completely the crown of leaves to which it delivers water. Nothing is of more fundamental importance in the plant than this vascular system, for without it the plant would be like an animal without a circulatory system. When *Zamia* is decapitated, therefore, the top of this vascular system is cut off, and the cylinder becomes an open, mutilated tube. Vascular tissue is the most per-

manent tissue in the plant body, and therefore least capable of cell division, but when regeneration begins in *Zamia* this mutilated vascular system is mended first, new vascular tissue being formed which connects with the remaining tissue and domes over the cylinder again. After the cylinder is completely restored, the new crown of leaves begins to appear, and soon the plant is complete again.

This illustration shows that regeneration is not necessarily a superficial process, resulting in an excrescent growth over a deformed interior, but it is first an internal reconstruction, followed by the normal development of external organs.

Some recent developments in connection with grafting are of interest in this connection. When one kind of plant is grafted upon another, the process by which the mutilated tissues become knit together into a continuous living body is a process of regeneration. The plant into which the graft is inserted is called the *stock*, and the inserted graft is called the *scion*. It has always been a question as to the mutual influence of stock and scion. They are different kinds of plants, with different leaves, flowers, and fruits, but in general each produces its own characteristic structures, although they have become parts of one body.

In comparatively recent times, however, attention has been called to what are termed "graft hybrids," which means that the scion takes on some of the characters of the stock, and thus becomes a hybrid. The most interesting fact in reference to these hybrids is that the tissues of the two parent plants remain distinct. Sometimes the graft hybrid is a mosaic of the two parent plants, the tissues from the two distinct origins being related to one another in patches. But most interesting are those graft hybrids in which the tissues from one parent invest those from the other parent as a mantle. Externally, therefore, such a hybrid resembles one of the parents exactly, but internally its whole structure is that of the other parent, and each region produces the structures peculiar to itself. Such composite plants are called "chimaeras," and they deserve the name. It is certainly a wonderful structure that combines in one organic whole tissues received from two sources, and which remain distinct. To graft one plant into another, therefore, may mean the production of a new kind of individual, one that is not an ordinary hybrid, inheriting qualities from one parent or the other, but combining the structures of both, one being the mantle of the other, and each doing its own work.

In conclusion, it may be said that the power of regeneration is as extensive as are living cells, and its results are as various as are the structures of the body. Not only can it restore lost parts to a mutilated structure, make a new structure to replace one that is lost, and call into activity dormant structures that have been held in check by the vigor of other parts, but it can also take two individuals and make a composite organism in which neither individuality is lost, but both live together as one body.